Deterministic and stochastic processes lead to divergence in plant communities 25 years after the 1988 Yellowstone fires

Running head: Postfire forest community development

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SUBMITTED TO ECOLOGICAL MONOGRAPHS

Abstract. Young, recently burned forests are increasingly widespread throughout western North America, but forest development after large wildfires is not fully understood, especially regarding effects of variable burn severity, environmental heterogeneity, and changes in drivers over time. We followed development of subalpine forests after the 1988 Yellowstone fires by

periodically re-sampling permanent plots established soon after the fires. We asked two questions about patterns and processes over the past 25 years: (1) Are plant species richness and community composition converging or diverging across variation in elevation, soils, burn severity, and post-fire lodgepole pine (*Pinus contorta* var. *latifolia*) density? (2) What are the major controls on post-fire species composition, and has the relative importance of controls changed over time? For question 1, we sampled 10-m^2 plots (*n*=552) distributed among three geographic areas that differ in elevation and substrate; plots spanned the spectrum of fire severities and were re-sampled periodically from 1991-2013. For question 2, we sampled 0.25-ha plots (*n*=72), broadly distributed across areas that burned as stand-replacing fire, in 1999 and 2012. Richness and species composition diverged early on between infertile low-elevation areas (lower richness) and more fertile high-elevation areas (greater richness). Richness increased rapidly for the first five years post-fire, then leveled off or increased only slowly thereafter. Only 6% of 227 recorded species were non-native. Some annuals and species with heat-stimulated soil seed banks were associated with severely burned sites. However, most post-fire species had been present before the fire; many survived as roots or rhizomes and regenerated rapidly by sprouting. Among the 72 plots, substrate, temperature, and precipitation (the abiotic template) were consistently important drivers of community composition in 1999 and 2012. Post-fire lodgepole pine abundance was not significant in 1999 but was the most important driving variable by 2012, with a negative effect on presence of most understory species, especially annuals and shade-intolerant herbs. Burn severity was significant in 1999 but not in 2012, and distance to unburned forest had no influence in either year. The 1988 fires did not fundamentally alter subalpine forest community assemblages in Yellowstone, and ecological memory conferred resilience to high-severity fire.

Key words: succession; disturbance; diversity; richness; composition; Rocky Mountains; subalpine forests; multi-level models; lodgepole pine; Pinus contorta

INTRODUCTION

Young, recently burned forests are becoming increasingly widespread throughout western North America. Annual area burned began to increase substantially in the mid-1980s, and climate models indicate that this trend will likely continue or even accelerate in coming decades (Westerling et al. 2011, Barbero et al. 2015). The growing prevalence of young forests on western landscapes has important implications for many ecosystem services (Swanson et al. 2011, Turner et al. 2013), and underscores the relevance of widely debated theoretical issues relating to community and ecosystem responses to disturbance (White and Jentsch 2001, Turner 2010). Forest development after large wildfires is not fully understood, especially regarding effects of variable burn severity, environmental heterogeneity, and changes in controlling mechanisms over time. We have followed development of subalpine forests after the 1988 Yellowstone fires—one of the first of the large wildfires that have come to characterize modern fire regimes—by periodically re-sampling permanent plots established soon after the fires. In temperate forests, understory vegetation is especially important, as it encompasses most of the diversity in the plant community (Gilliam 2007) and may be especially sensitive in its response to disturbance (Roberts 2004). Here we report plant community dynamics from the first 25 post-fire years to evaluate the patterns and processes by which these forest communities have re-developed across the heterogeneous Yellowstone landscape.

A fundamental question about patterns of succession is whether initially distinct post-disturbance plant communities tend to *converge* on a similar composition over time, as environmental constraints and competitive species interactions winnow out a random suite of early colonizers (e.g., Margalef 1968), or if communities tend to *diverge* over time as initial random colonizing effects persist and spatially heterogeneous abiotic filters exert ever greater influences (Walker et al. 2010, Siegwart Collier and Mallik 2010, Harvey and Holzman 2014, Brown et al. in press). Although Clements' early notion of unidirectional succession to a climax has been thoroughly debunked (Christensen 2014), more nuanced concepts of convergence and divergence remain pertinent. It appears that divergence is the norm where initial differences in abiotic conditions or disturbance severity are relatively great or when biotic residuals (and thus ecological memory—Johnstone et al. *in review*) are abundant (Turner et al. 1998, Franklin et al. 2000, Roberts 2004), but that convergence may occur where disturbances are less severe, abiotic conditions are more similar, or the available species pool is small (Glenn-Lewin and van der Maarl 1992)

Divergent successional trajectories have been documented in a wide variety of ecosystems, ranging from abandoned agricultural fields (Baeten et al. 2010) and boreal forests (Hart and Chen 2008, Shenoy et al. 2011), to dune fields (Ransjin et al. 2015) and marine intertidal or subtidal zones (Sousa 1984, Breitburg 1985). But convergence/divergence patterns can be subtle, depending on spatial scale and type or intensity of disturbance. Following the volcanic eruption of Mt. St. Helens, major differences in species composition were seen initially among groups of plots distributed along a 262 m elevational transect, due to substantial variation in local environmental conditions and differential establishment of one particularly influential

species; these differences along the gradient persisted throughout the first 26 years of primary succession (del Moral 2007). However, plots in close proximity (<250 m), and therefore relatively similar in local abiotic conditions, exhibited convergence in species composition during this period (del Moral 2007). In a cool-temperate forest in northern Michigan, tree species composition became more similar over 70 years within small patches having relatively homogeneous abiotic conditions (10-100 m scale), but diverged between patches in different abiotic settings (Woods 2007). Following experimental N fertilization of old-field vegetation in Minnesota, sets of plots that received substantially different amounts of N diverged in species composition over 11 years, while replicate plots that received the same amount of N developed more similar species composition, especially in younger fields (Inouye and Tilman 1995). In a low-productivity grassland in Michigan, a one-time experimental reduction in total biomass was followed by compositional convergence among previously dissimilar plots, but continuous fertilization led to divergence into three distinct community states (Houseman et al. 2008).

Both convergence and divergence may be seen in a single area at different times over the course of succession. Understory species compositions were spatially variable before logging and burning of Douglas-fir forests in Oregon (USA), but convergence in species composition was seen on drier sites immediately after disturbance, as a suite of widely distributed colonizers flourished throughout the disturbed areas (Halpern 1988). However, community composition soon began to diverge as the early colonizers, many of which were annuals or biennials, declined in abundance, and as pre-disturbance species recovered via sprouting or seed germination.

Questions of divergence and convergence also can apply to community properties other than species composition, e.g., plant functional traits or species richness irrespective of which particular species are present. Numerous studies have documented convergence in plant growth forms and functional traits among plots that initially differed in these characteristics—annual vs. perennial, plant height, leaf distribution along stems, vegetative spread, period of flowering, seed mass—while species compositions of those plots showed no such convergence. Examples include natural succession on abandoned agricultural lands (Kahmen and Poschlod 2004, Myster and Malahy 2008) and trajectories of experimental grasslands where initial composition was varied by the investigators (Fukami et al. 2005). Species richness also has been observed to converge across plots that initially had more or fewer species. On Mt. St. Helens, species richness initially was much lower on a more severely disturbed site, but after 25 years, richness on the severely disturbed site was approaching—i.e., converging on—richness of the less severely disturbed site (Carey et al. 2006). A similar trend of increasingly similar richness among plots was seen in abandoned pastures in Puerto Rico (Myster and Malahy 2008) .

A second fundamental question relates to the ecological processes underlying successional patterns: what is the relative importance of deterministic vs. stochastic driving variables, and how do the influences of these variables vary in time and space? Deterministic drivers are those that involve non-random, niche-based mechanisms, e.g., plants' physiological responses to local climate and soils, whereas stochastic drivers such as dispersal from a regional species pool or severity of disturbance give rise to patterns indistinguishable from random chance (Chase and Myers 2011). Deterministic drivers can be viewed as environmental filters, and stochastic drivers also are referred to as neutral effects (e.g., Chase 2007, Murphy et al.

2015). Clearly, both kinds of controls can influence the development of plant communities (Myers and Harms 2011). Deterministic variables related to soil and climate must always be important, for they determine which species are biologically capable or incapable of surviving in a given place. Stochastic drivers may be equally influential in some cases, but the relative importance of stochastic variables, e.g., size and composition of the regional species pool and dispersal characteristics of those species, or the severity of disturbance, may vary with environmental context and scale of analysis.

Chase (2007) observed greater compositional similarity among pond communities subjected to drought and less similarity under more benign conditions of average moisture. He interpreted this as stronger niche-selection and environmental filtering of species dispersing in from the regional species pool under the harsh conditions of drought, but a greater influence of stochastic dispersal when the environmental filters were less stringent. In Australian forests and shrublands, spatial patterns of species distributions and of community species diversity are influenced by both deterministic (soil nutrients, water availability) and stochastic (fire history) variables, with the deterministic variables having important effects at all scales of analysis and the stochastic variables becoming more conspicuous at finer spatial scales (Perry et al. 2013, Cohn et al. 2015).

Other stochastic influences also have been documented. Following cessation of intensive agriculture in eastern North America and northern Europe, local species assemblages and trajectories of compositional change have varied in response to fine-scale spatial variation in seed sources, herbivore pressure, the specific time of field abandonment, and weather conditions

at key periods of plant development such as seed set and dispersal (Pickett et al. 2001, Baeten et al. 2010). After grazing was terminated in a Danish heathland, two distinct successional trajectories developed over the next 100 years—a shrub- or a grass-dominated version. The trajectory in any particular place was predicted not by local soils properties (a deterministic control) but by whether grasses already had been present on that site at the time of grazing cessation, which in turn was a stochastic function of historical soil disturbance (Ransjin et al. 2005). Colonization by particular species of sessile marine organisms after experimental disturbance of existing communities or provision of new substrates was strongly influenced by stochastic factors such as whether colonization began in spring or in summer, and the size of the disturbed patch, which influenced the intensity of grazing pressure on early colonists (Sousa 1984, Breitburg 1985). Unpredictable stochastic events like severe drought or storm also can introduce new compositional variation into an already established successional trajectory, either in a natural setting (Yurkonis and Meiners 2006, Woods 2007) or in an experimental plant community (Kreyling et al. 2011).

The relative influence of deterministic vs. stochastic driving variables may change over the course of succession, with deterministic variables apparently increasing in importance. Species distributions were associated with narrower ranges of soil pH in older stands than in younger stands developing after abandonment of agricultural fields, suggesting that deterministic variables like soil pH become increasingly important as stands develop (Christensen and Peet 1984). Gilbert and Lechowicz (2004) explained fine-scale heterogeneity in herbaceous-layer composition of an old-growth temperate forest almost entirely by deterministic variables such as soil chemistry, topographic aspect, and light availability. Whether deterministic or stochastic, the

relative importance of various drivers changes over the course of succession as the organisms modify the abiotic environment. In primary succession on Alaskan river floodplains, for example, there is a shift from mainly physical controls to increasingly important biological controls once a shrub stage forms a closed canopy, which increases shade and also nitrogen availability if the dominant shrub is alder (Chapin et al. 2005).

In our study we regarded deterministic variables as those that are relatively consistent, predictable, and measurable—viz., local soil characteristics and average local climate conditions. We regarded stochastic variables as those that are relatively random and unpredictable—viz., local burn severity, local seed bank, and spatially variable development of post-fire tree cover (which was itself contingent on prevalence of serotiny in the pre-fire stand and burn severity; see Turner et al. 1997, 1999, 2003a). Based on periodic re-sampling of permanent plots from 1991-2013 throughout the subalpine areas burned in the 1988 Yellowstone fires, we evaluated the patterns and processes of post-fire subalpine forest community development by asking two questions:

*(1) Convergence or divergence: Are plant species richness, community composition, and plant morphological type, converging or diverging across variation in elevation, soils, burn severity, and post-fire lodgepole pine (***Pinus contorta *var.* latifolia***) density?* We hypothesized that:

H1a: Species richness would be low initially in all burned areas but would increase over time in all areas.

H1b: Community composition would be similar initially in all geographic areas, but would diverge over time with variation in elevation, soils, climate, and post-fire lodgepole pine density.

H1c: Within any given geographic area, the most severely burned sites initially would support lower richness and different community composition than less severely burned sites, but sites of different burn severity would converge in richness and composition over time.

H1d: A great variety of plant morphological types would be represented in the earliest post-fire communities, but the variety of traits would decrease over time (i.e., converge) within local communities and across the burned landscape, regardless of convergence or divergence in species composition.

(2) Processes: What are the major environmental controls on post-fire species composition, and has the relative importance of controls changed over time? We hypothesized that:

H2a: Burn severity (a stochastic variable) would be an especially important control initially, but would become less important over time.

H2b: The "abiotic template"—local substrate, elevation, and climate (all deterministic variables)—would be a relatively unimportant control on community composition initially, and would become increasingly important over time.

H2c: Distance from unburned forest (a stochastic variable, related to potential seed source for recolonizing species) would be important initially but become less important over time.

H2d: Post-fire lodgepole pine density (a stochastic variable) would be a relatively unimportant control on community composition initially, but would become increasingly important over time.

STUDY AREA AND METHODS

Study area

Yellowstone National park (YNP) is located in northwestern Wyoming and adjacent parts of Idaho and Montana, USA. The park covers ca. 9,000 km^2, centered on a high (elevation ca. 2100-2700 m) volcanic plateau. Most of the area is underlain by infertile rhyolite substrates, although somewhat more fertile andesites and lake bottom sediments are present in places. Approximately 80% of YNP is dominated by lodgepole pine forest. Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) are locally abundant at higher elevations. At lower elevations, Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) forests grade into sagebrush (*Artemisia* spp.) steppe and grasslands. The climate is characterized generally by cold, snowy winters and dry, mild summers.

Fires in 1988 burned ca. 570,000 ha in YNP and surrounding lands (Schullery 1989). Fire weather was extreme, with high winds and lightning but no rain. Fire suppression efforts were effective in protecting most human life and property, but the fires could not be stopped until snow came in mid-September (Schullery 1989). The fires were not only extensive, but also very heterogeneous in their effects on the vegetation (Turner et al. 1994, 1997). The initial post-fire

landscape was a mosaic of patches of varying burn severity and varying legacies (e.g., surviving plants, litter, and coarse wood) of the forests that burned.

We characterized burn severity into three classes (Turner et al. 1997). *Crown fires* were of highest severity, burning on the ground and through the forest canopies, killing all of the trees, consuming needles and small twigs, killing all above-ground plant parts, and consuming all of the O horizon and a portion of the coarse dead wood on the ground; these places were typically covered with gray ash after burning. *Severe surface fires* were of intermediate severity, burning on the ground, generating enough heat to kill all of the canopy trees but not consuming the needles or small twigs in the canopy, killing all above-ground plant parts, and consuming most of the O horizon and some coarse dead wood; the canopy typically retained red dead needles for 2-3 yr, which gradually produced a layer of dead needles on the forest floor. Crown fires and severe surface fires were both stand-replacing. *Low severity surface fires* burned small patches of litter and small dead branches on the forest floor, but did not injure most of the trees and understory plants; these places retained most of their pre-fire characteristics although small patches of mineral soil were exposed by the localized burning.

Total plant cover increased rapidly through the first five years after the fires, then leveled off or continued to increase more slowly (Turner et al. 2003a). Lodgepole pine seedlings established within the first two years after the fires at densities equaling or (most commonly) well exceeding pre-fire density in almost all of our sampling areas (Turner et al. 1997). Quaking aspen seedlings (*Populus tremuloides*) also established in some of the burned area during the first two years post-fire; subsequently these seedlings have persisted and grown larger, though

density has decreased (Hansen et al. 2016). The small lodgepole pine seedlings had no apparent competitive influence on post-fire herbs or aspen seedlings during the first decade post-fire (Anderson and Romme 1991, Romme et al. 2005), but since 2000 the pines have grown into small trees and formed a closed canopy in many areas.

Field methods

We developed long-term datasets, representing different spatial scales of post-fire heterogeneity (Table 1):

Question 1: Convergence or divergence. In each of three geographic areas in YNP that differed in elevation and substrate, we established long-term vegetation plots in a large (10^3 ha), moderate (10^2 ha), and small (10^0 ha) burned patch (total of nine patches; Table 2, Figure 1). Each patch was centered on an area burned as crown fire in 1988 and patch size was calculated as the area of stand-replacing fire (crown plus severe surface fire). Patches also contained areas of low-severity surface fire (Table 2; see Turner et al. 1997 for more detail on study design).

Within each patch, transects running in the four subcardinal directions from the center to the edge (unburned forest) of each patch were established initially in 1990, two years after the fires. Sampling occurred at varying distances (20 to 200-m intervals) along each transect in 1990, 1991, 1992, 1993, 1996, and 2000, with plots positioned to capture variation in burn severity and distance from unburned or less severely burned forest. Plots were marked by stone cairns and wooden stakes and locations documented with GPS. Trends in post-fire tree density and percent cover of functional groups (e.g., graminoids, forbs) were reported previously (Turner et al. 1997, 2003). We also recorded the presence of plant species in 10-m^2 plots at each sampling location (*n*

= 552) beginning in 1991. A 10-m tape was centered on the wooden stake and extended perpendicular to the transect, and a second tape was laid out 1-m beyond and parallel to the first transect. All plant species rooted within the 10-m^2 sampling plot were recorded each year.

We intended to re-sample all of the patches in 2013, but this proved infeasible due to the dense cover of post-fire lodgepole pine and fallen fire-killed trees that had developed by this time in most areas, interfering with travel along the sampling transects and obscuring the cairns marking the permanent 10-m^2 plots. However, we re-located and again recorded species richness and composition in 14 severely burned 10-m^2 plots in the center of the large or moderate patch at each of the three geographic locations in 2013, 25 years after the fires. Here, we report species richness and composition data from all nine patches from 1991 to 2000 and in the severely burned patch centers from 1991 to 2013 (Table 1).

Question 2 – Processes. Plots (n = 90, 0.25-ha) were established in 1999 (post-fire year 11)—stratified to represent a wide range of post-fire lodgepole pine densities, elevations, and substrate conditions, and restricted to locations 0.1-1.0 km from a road or trail or lakeshore to reduce human impacts but permit reasonable access—and randomly distributed throughout the area burned in 1988 (Figure 1; Turner et al. 2004). Plots were 50 m x 50 m in size, oriented toward the north. Post-fire tree density, size and productivity were measured along three 50 m x 2 m belt transects as described in Turner et al. (2004). We re-sampled 72 of these plots in 2012 (post-fire year 24) using the same methods. Changes in tree density, size, and productivity between 1999 and 2012 are reported in Turner et al. (2016a). In 1999 and 2012, we also recorded presence and percent cover of all species within 0.25-m^2 quadrats (n = 25) placed at 5-m

intervals along the transects. We tallied all plant species that were recorded in the 25 quadrats and analyzed the species assemblage in each plot for both time periods. The sampled area in each year for the species list and analysis was only 6.25 m^2 per plot, but in 2012 we tallied all species within the entire 0.25-ha plot and found that the 25 quadrats captured ca. 95% of the species in a plot, missing only a few rare species.

Environmental covariates. For the patches (Question 1), we obtained elevation (m above sea level) and geological substrate data at the patch level from maps and GIS databases (Table 2). Burn severity (crown fire, severe surface fire, low severity surface fire, as in Turner et al. 1997, 1999) was classified in the field in 1990, when severity classes were still visually conspicuous.

For the 72 0.25-ha plots (Question 2), topoedaphic covariates included elevation and substrate, which was grouped into four categories, according to physical characteristics of the soil and their expected effect on vegetation. Ranked numerically from least to most fertile based on nutrient status and water-holding capacity (Turner et al. 2004), substrate categories included (1) rhyolite till, which occurs on uplands and is derived from rhyolite-based glacial till; (2) rhyolite glacial, located on glacial outwash plains; (3) rhyolite low-base saturation, occurring on lake plains and derived from rhyolite-based glacial rubble; and (4) andesite, including soils derived from andesite, as well as alluvial deposits. All plots were in stand-replacing fire, but we obtained more precise measures of local 1988 burn severity from the Monitoring Trends in Burn Severity database (MTBS; Eidenshink et al., 2007; www.mtbs.gov). We used the differenced Normalized Burn Ratio (dNBR), which is an appropriate index of burn severity when all study

sites had similar pre-fire vegetation. To avoid interpolation errors when projecting dNBR to the UTM for plot center, we used a 3 x 3-window smoothing algorithm on the dNBR layer. We calculated distance from each plot to the nearest unburned forest (defined as dNBR < 100 on the 30-m resolution dNBR map) in ArcMap. Gridded PRISM data (4-km resolution) were used to calculate mean annual temperature and precipitation for the decade prior to 1999 and the decade prior to 2012 for each plot (PRISM Climate Group 2014). Slope and aspect were not included because plots were on flat terrain to eliminate these potentially confounding effects. See Appendix S1 for mean values.

Data analyses

Question 1: Convergence or divergence. For species richness, we compiled the number of species in every 10-m^2 plot, then tallied the number of species recorded in all 10-m^2 plots within a patch, within all patches in a geographic area, and within all 552 plots sampled throughout our study area. This compilation was done for each year of sampling. Because sample size was unequal among geographic areas and patches (Table 2), we generated rarefaction curves for each geographic area and for each patch by year (Gotelli and Colwell 2011, Colwell et al. 2012). Comparisons of species richness among years were based on rarefaction curves using the largest sample size shared among all comparisons (see Appendix S2). For analysis of functional diversity, we classified species by morphological type (trees, shrubs and subshrubs, perennial forbs, short-lived forbs--annuals, biennials, and short-lived perennials—and perennial graminoids; see Appendix S3). We compiled the number of species in each category and computed Bray-Curtis indices of dissimilarity (Bray and Curtis 1957).

To visualize similarities and differences among the plant communities sampled, we ordinated plots in species space via nonmetric multidimensional scaling (NMS). Analyses included only those species present in at least 5% of all plots over all sampling years to diminish the sway of rare species. All community-related statistics shown were executed using PC-ORD ver 6.15 (McCune and Mefford 2011). To determine how plant community composition may be controlled by the environment, we correlated NMS axes with the variables of elevation (m), burn severity class (ordinal: 0, 1, 2, 3) in order of increasing severity), and lodgepole pine density (stems ha^{-1}). The large quantity of observations precluded displaying individual points in ordination space. Therefore, our ordination plots display the group mean values with error bars that represent the inter-quartile range surrounding the mean.

To quantify whether groups were converging or diverging with time, we employed multiple response permutation procedures (MRPP), which determine how distinct a selected group is. The MRPP test yielded the A-statistic, which ranges from -1 to 1, where 0 corresponds to a group that is no different from the random assumption; within-group similarity (how distinct a group is from a randomized data set) increases as A approaches 1, and negative values indicate a group that is more heterogeneous than the random assumption (McCune and Grace 2002).

To determine which species may be driving potential trends shown with the NMS and MRPP data, we also performed an indicator species analysis (Dufrene and Legendre 1997) in PC-ORD6 using the phi-statistic of Tichy and Chytry (2006). Phi ranges from -1 to 1, where 1 corresponds to a species that is present in all sites of a given group and is absent in all others, and -1 corresponds to the opposite scenario. We conducted Monte Carlo tests of significance for the maximum observed value for each species.

Question 2: Processes. We used multilevel models (MLMs; Gelman and Hill 2007) to analyze differences in species presence among the 72 broadly distributed plots in 1999 and 2012. The strength of MLMs is their ability to integrate species- and community-level analyses into the same model (Jackson et al. 2012). Multilevel models can separate effects of collinearity among environmental drivers and factor out effects of changes in overall species occurrences that do not involve changes in composition (Jackson et al. 2012). In addition to providing information about community composition, MLMs simultaneously identify individual species' responses to the environmental variables. Thus, MLMs not only have superior statistical properties in analyses of community composition compared to existing methods, but they simultaneously provide detailed information about species-specific responses underlying the changes in community composition (Jackson et al. 2012). The MLM allows estimation and statistical tests for variation among species in their response to different environmental predictors. The MLM can be interpreted as a set of logistic regressions in which difference in slopes and intercepts among species are random variables (Gelman and Hill 2007, Jackson et al. 2012).

The MLMs were run separately for each year. The presence of each species was the response (dependent variable) and environmental variables were the predictors (independent variables). Environmental variables for each plot included substrate, elevation, mean temperature during the previous 10 yr, mean precipitation during the previous 10 yr, burn severity, lodgepole pine density, and lodgepole pine aboveground net primary production (ANPP; Turner et al. 2004, 2016a). All environmental variables were transformed by subtracting the mean and dividing by the standard deviation, so that each variable had mean zero and variance 1; this makes it possible to compare regression coefficients within the same model directly because they measure effect

sizes. To reduce the number of variables in the MLM, we used Akaike's information criterion

(AIC) for model selections, always including the fixed effect β for an environmental variable if

the corresponding random effect $e_{spp(i)}$ was included. All MLM analyses were performed using

lmer in R version 2.8.1 (R Development Core Team 2008) using code modified from Jackson et

al. (2012).

Comparing pre- and post-fire species assemblages: Overall, our impression was that, after

25 years, post-fire spatial patterns of community composition in Yellowstone's subalpine forests

strongly resembled pre-fire patterns. To test this idea, i.e., to quantify the similarity of pre- and

post-fire community spatial patterns, we drew upon two sources to estimate pre-fire species

assemblages in our three geographic areas (pre-fire floristic data specific to our study areas were

not available). First, we tallied the indicator species of mature forests identified in forest "habitat

types" of the region. A habitat type is "a set of environmental conditions that appears repeatedly

across a landscape" and is "named after the climax community that would develop on that site

after sufficient passage of time" (Despain 1990). We reject the climax concept, but the species

listed as indicators of particular habitat types do represent species thought to be especially

characteristic of mature forest communities within a particular abiotic template. By examining

habitat type distribution maps that included the three geographic areas of our study (Steele et al.

1983, Despain 1990), we compiled the indicator species that would typify mature pre-fire

communities in each area. Our second source of pre-fire compositional data came from

unpublished species lists that we have compiled as part of other studies in unburned forests of

YNP where the environmental context was similar to one of the three geographic areas in our

present study. After compiling these lists of species that characterize mature forests in each

geographic area, we determined whether we had recorded those species in our post-fire sampling (our full patches data-set, Table 1).

RESULTS

Question 1 – Convergence or divergence of richness and composition:

We recorded a total of 227 species between 1991 and 2013 in the subalpine forests that burned in 1988 (Appendix S3). Of these, only 13 (6%) were non-native. All but two of the species we encountered had been recorded in YNP before the fires; we found a previously undocumented native perennial forb, *Hedysarum alpinu*m, and a new non-native annual forb, *Filago arvense*. The 227 species represented a variety of morphological types (Appendix S3).

H1a: Species richness. In our full data-set from 1991-2000 (n=552 plots, Table 1), there was a substantial increase in the number of species recorded from 1991 to 1993, then a much slower increase or leveling off thereafter. Rarefied number of species was consistently greatest at the relatively fertile, highest elevation Lake area, and lowest at the infertile and lower-elevation Cougar and Fern areas (Figure 2, Table 2). Within any single geographic area, there were no consistent differences in species number in relation to patch size (Figure 3). We saw no evidence of convergence in richness among geographic areas: the most fertile, high-elevation area always had greater richness than the less fertile study areas at low to intermediate elevations. Nor was there any strong pattern of convergence among patch sizes within a geographic area, except perhaps weakly so at the Lake area where the large patch had a relatively low species number in 1991 but from 1993-2000 had a similar number of species as the other two patches (Figure 3)

We also evaluated richness patterns in the severely burned centers of the large or moderate patch in each geographic area that were re-sampled periodically from 1991-2013—a smaller set of plots ($n = 42$) but our longest time-series (Table 1). At the finest spatial scale, mean number of species per 10-m^2 plot, richness increased steadily from 1991-2000, but changed little thereafter (Figure 4a). Scaling up to the number of species in each geographic area, we again saw increases from 1991-2000, after which the two infertile, lower-elevation areas (Cougar and Fern) leveled off, but species number continued to increase through 2013 at the more fertile, highest-elevation Lake area (Figure 4b). Combining the species tallied among all three geographic areas, total species number increased through 2000 and then leveled off (Figure 4c). Consistent with the patterns seen in the full data-set from 1991-2000 (Figure 3), this smaller but longer data-set showed no evidence of convergence in richness among geographic areas, and the more fertile, higher-elevation Lake area had more species than the infertile, lower-elevation Cougar and Fern areas in almost every year (Figure 4b).

H1b: Community composition among geographic areas. Community composition already was relatively distinct in each geographic area in 1991 and remained distinct throughout the first decade after fire (NMS species presence/absence ordination of our entire data-set from 1991-2000; Figure 5a). In fact, the inter-quartile ranges surrounding the means of each geographic area do not overlap at all in ordination space (Figure 5a). Within-group Sorensen distance (δ) among 10-m^2 plots decreased over time in each of the three geographic areas (Table 3a), indicating that community composition became more homogeneous within a geographic area from 1991-2000. The centroids in all three areas generally move to the right in ordination space, reflecting the continuing accumulation of new species, but they do not converge in composition.

Elevation increases toward the top and right-hand portions of Figure 5a, post-fire lodgepole pine density increases toward the bottom and left (Table 3b), and the three geographic areas sort out accordingly: the Cougar area is at lowest elevation and has plots with the greatest post-fire lodgepole pine densities; the Fern area is intermediate in elevation and lodgepole pine densities; and the Lake area is at highest elevation with many plots having very low lodgepole pine densities. Several species were strongly associated with a particular environmental setting, e.g., the shrub *Ceanothus velutinus* was found only at Cougar and is located far to the lower left in ordination space, whereas *Epilobium ciliatum* and *Calamagrostis canadensis* were most commonly recorded at Lake, and are in the upper right portion of ordination space (Figure 5a). Most species, however, were found with varying frequency in all three geographic areas, and are clustered in the middle portion of ordination space, e.g., *Agoseris glauca* and *Polygonum douglasii* (Figure 5a).

The same pattern is seen in NMS ordination of the severely burned plot centers, which is our smaller but longer dataset (14 10-m^2 plots per geographic area, Table 1). Composition of severely burned plots was distinct in each geographic area at the outset (1991), and remained so through 2013 (Figure 5b). In this figure, elevation increases toward the top and left-hand portion of ordination space; lodgepole pine density increases toward the bottom and right (Table 3c). As with the ordination of the full data-set from 1991-2000 (Figure 5a), in this analysis the three geographic areas do not overlap in ordination space (Figure 5b). Two species centered in the far left-hand portion of ordination space, *Geum macrophyllum* and *Ranunculus uncinatus*, were recorded only at the fertile, high-elevation Lake area, but none of the species depicted in Figure 5b were restricted to the infertile Fern or Cougar areas.

H1c: Community composition among burn severity classes. Differences among fire-severity classes as quantified by MRPP from 1991-2000 were statistically significant ($p <$ 0.00001), in part because of large sample sizes, but the A-statistic was small (≤ 0.20) in every comparison, indicating little compositional differentiation in relation to burn severity (see Appendix S4).

Despite the lack of strong patterns in the MRPP analysis, the indicator species analysis suggested some modest compositional differences among burn severity classes (Table 4). In all three geographic areas the indicator species for low-severity burns were trees (seedlings plus surviving adults) plus perennial forbs and graminoids common in unburned forests; in contrast, indicator species for the most severe burns were either perennials that had been locally rare or absent before the fire but had heat-stimulated soil seed banks, or annuals and short-lived perennials that establish preferentially on bare mineral soil.

H1d: Diversity of plant morphological types. The 10-m^2 plots in the severely burned centers of the large or moderate patch in each geographic area (Table 1) had a relatively distinctive makeup of morphological types in 1991 and again in 2013 (Table 5a). The Bray-Curtis index of dissimilarity for proportions of morphological types fluctuated somewhat between years, but was moderately high in every comparison (0.57 – 0.65), with no strong temporal trends (Table 5b). In both 1991 and 2013, long-lived perennial forbs predominated in all three areas (roughly half of the species present). However, the infertile, low-elevation Cougar area was characterized by the greatest proportion of shrub and subshrub species, the infertile, intermediate-elevation Fern area by the greatest proportion of graminoids, and the more fertile,

highest-elevation Lake area by the greatest proportion of tree species (although total tree density at Lake was lower than at the other two areas).

Question 2 - Environmental controls and changes in relative importance over time:

For each year, we analyzed species found in at least 5% of the 72 plots, excluding rarer species for which sample size was inadequate. A total of 58 species met this criterion in 1999, 11 years post-fire, and 52 species did so in 2012, 24 years post-fire. Species lists in the 72 plots generally mirrored species lists in the patches, indicating that the datasets applied to our two overarching questions represented similar species pools and environmental contexts, all broadly representative of the Yellowstone subalpine plateaus. The most conspicuous change in stand structure between post-fire years 11 and 24 in the 72 plots was a substantial increase in density, biomass, and productivity of lodgepole pine (Turner et al. 2016a). MLM analyses revealed that different suites of variables controlled species composition in 1999 and in 2012 (Tables 6, 7). In both years, the best fitting MLM had no competing models with ΔAIC < 2.

Controlling variables in post-fire year 11. MLM results include fixed effects related to the likelihood of all species occurring in a particular area (roughly analogous to richness), and random effects, which predict occurrence of individual species. Five variables—substrate, lodgepole pine ANPP, precipitation, burn severity, and mean annual temperature—were significant fixed effects in 1999, with substrate being most important. Any species was more likely to occur in plots on more fertile substrates, with lower lodgepole pine ANPP, with less precipitation, greater burn severity, and warmer temperature (Table 6a). Among-species variation in presence, indicated by random effects in the MLM analysis, was explained in post-

fire year 11 by environmental variables associated with substrate and climate (Table 6a). Among individual species, substrate had a strong influence (random effects coefficients $\geq$ |0.20|) on 67% of the 58 species, with 36 species more likely to occur on more fertile substrates and 3 species more likely to occur on less fertile substrates (Table 6b). Among predictors, substrate was the most important (highest coefficient) for 36 of the 58 species. Mean annual precipitation for the preceding decade was a strong influence on 64% of the species, with all except one species more likely to occur where precipitation was lower. Mean annual precipitation was the most important predictor for only 15 of the species. Mean annual temperature for the preceding decade was a strong influence on 41% of the species, and it was the most important predictor for 8 species (Table 6b).

Controlling variables in post-fire year 24. Four variables—lodgepole pine density, substrate, mean annual precipitation, and mean annual temperature—were significant fixed effects in 2012, with lodgepole pine density now the most important. Any species was more likely to occur in plots with lower lodgepole pine density, on more fertile substrates, with less precipitation, and warmer temperature (Table 7a). Among-species variation in presence, as indicated by random effects in the MLM analyses, was still influenced by environmental predictors related to substrate and climate, but lodgepole pine density became the most important controlling variable (Table 7a). Among individual species, lodgepole pine density had a strong influence (random effects coefficients $\geq$ |0.20|) on 77% of the 52 species, with 38 species more likely to occur where pine density was lower and two species more likely to occur where pine density was higher (Table 7b). Among predictors, lodgepole pine density was the most important (highest coefficient) for 27 of the 52 species. Substrate had a strong influence on 69% of the

species, with 34 species more likely to occur on more fertile substrates and two species more likely to occur on less fertile substrates (Table 7b). Substrate was the most important predictor for 16 species. Mean annual precipitation had a strong influence on 58% of the 52 species, with 26 species more likely to occur where precipitation was lower and four species more likely to occur where precipitation was higher. Precipitation was the most important predictor for four species. Elevation had a strong influence on 52% of the 52 species, with 12 species more likely to occur at higher elevations and 15 more likely to occur at lower elevations. Elevation was the most important predictor for four species. Mean annual temperature had a strong influence on 69% of the 52 species, with 28 more likely to occur in warmer temperatures and eight more likely to occur with cooler temperatures. Temperature was the most important predictor for three species (Table 7b).

Evaluating the hypotheses. Comparing the MLMs between years allows each hypothesis to be evaluated. Burn severity (H2a) was significant in explaining patterns of species occurrence in 1999 (Table 6) but was no longer significant in 2012 (Table 7). The abiotic template (H2b) was significant in both time periods, having the strongest influence of all variables in 1999 and second only to lodgepole pine density in importance in 2012. Distance to unburned forest (H2c) had no detectable effect on patterns of species occurrence in either 1999 or 2012. And post-fire lodgepole pine density or productivity had no significant effect on species presence in 1999 but a very strong effect, often exceeding the influence of the abiotic variables, in 2012.

The numbers and characteristics of species that increased or decreased substantially in the 72 plots from 1999-2012 also were consistent with the increasing importance of the aggrading lodgepole pine canopies (Table 8). Only three species increased substantially, i.e., the proportion of plots in which they were recorded increased by $\geq$50%; all were perennials, and all were typical of mature forest environments. Twenty-one species became less abundant (decreased by $\geq$50%). Of these, four were short-lived forbs (annuals, biennials, or short-lived perennials), two were species typical of grasslands or other non-forest habitats, and two were relatively shade-intolerant forest species. Five species were relatively rare in 1999 (present in <10% of the plots), and all five of these were absent in 2012; one was an annual and one was typical of non-forest environments, as would be expected in an increasingly shady environment. However, the other three that disappeared from the plots were species of mature forests.

Comparing pre- and post-fire species assemblages: We documented the post-fire presence of the expected indicator or other characteristic species in 57 of 64 cases in our three geographic areas (Table 9). Three cases where a species was missing are explained by broad-scale species distribution patterns (these species actually would not be expected in our areas; see footnotes in Table 9). An interesting missing species after 1988 is *Picea albicaulis*, which was common in the Fern area before the fires—mostly as suppressed-appearing saplings—but was not recorded there in our post-fire sampling. The large wingless seeds of this high-elevation tree are dispersed by birds, sometimes from great distances (Tomback et al. 2001); the species had no local seed sources in the Fern area after the fires, so it may not re-appear in this area for a long time. Overall, aside from some interesting exceptions like *P. albicaulis*, this analysis confirmed our

impression that pre-fire spatial patterns of species assemblages were re-established quickly, within the first couple of decades after the fires.

DISCUSSION

Our study of post-fire plant community development during the first 25 years after the 1988 Yellowstone fires revealed rapid recovery of the native plant community. Species richness was low in the first post-fire year, especially in the most severely burned areas (Anderson and Romme 1991), but increased rapidly through post-fire year five and then more slowly through post-fire year 12, by which time richness had largely stabilized. Non-native species were uncommon, and their abundance declined during the first 25 years post-fire (Wright and Tinker 2012). Most herbaceous perennial species survived as roots and rhizomes, as mean depth of soil char was only 14 mm (Turner et al. 1999), then re-sprouted after the fire. A few species that had not been conspicuous in pre-fire communities also appeared in burned areas. For example, the shrub *Ceanothus velutinus* and the upland sedge *Carex rossi* established via heat-stimulated germination of local soil seed banks. In addition, several annuals and perennials that establish preferentially on bare soil and are rare in mature forests (e.g., *Gayophytum diffusum, Collinsia parviflora, Polygonum douglasii*) also established from the local seed bank or via wind dispersal. Biotic legacies such as survivors and seeds provide "ecological memory" that enhances forest resilience to disturbance (Franklin et al. 2000, Seidl et al. 2014, Johnstone et al., in review). Further, the suite of species traits present in a community constitutes an "information legacy" that also supports recovery to the pre-disturbance state (Pausas and Keeley 2014, Johnstone et al., in review). After 25 years, post-fire spatial patterns of community composition strongly

resemble pre-fire patterns, and our data suggest substantial resilience of native subalpine forest plant communities to large, high-severity fire.

Rapid post-fire recovery of the pre-fire plant community has also been documented in other ecosystems, suggesting that this may be typical in temperate coniferous forests. Examples include ponderosa pine-Douglas-fir (*Pinus ponderosa-Pseudotsuga menziesii*) forests in Colorado (Fornwalt and Kaufmann 2014, Abella and Fornwalt 2015), Douglas-fir dominated forests in Oregon (Donato et al. 2009), spruce-fir (*Picea engelmannii-Abies lasiocarpa*) forests in the Teton Range just south of YNP (Doyle et al. 1998), western red cedar-western hemlock (*Thuja plicata-Tsuga heterophylla*) forests in Idaho (Stickney 1986), and coastal serotinous pine forests in California (Harvey and Holzman 2014).

Post-1988 plant community dynamics in YNP's subalpine forests generally fit Egler's (1954) model of initial floristic composition. Some short-lived, shade-intolerant species did appear soon after the fire, and these declined over time with increasing shade and competition from the growing lodgepole pine canopy. However, we saw no indication that these early transient species were facilitating establishment of longer-lived, more shade-tolerant species (as described in Egler's relay floristics model). On the contrary, legacy effects appeared to dominate; species typical of mature forests appeared soon after the fire, via sprouting of surviving belowground parts and germination of soil seed banks. When looking at a wide range of stand ages it is possible to describe apparent stages of succession in YNP forests—an early herbaceous stage, a lodgepole pine stage, and a late spruce-fir stage—but the present study

shows that all of the major species establish soon after fire, and the "stages" reflect differential

growth rates of the various species rather than a true species turnover (Johnson and Fryer 1989).

A similar trend was seen after fire in Mediterranean-climate shrublands in California: all

of the shrub and subshrub species present before the fire were present one year post-fire either as

sprouting survivors or seedlings; numerous new species also appeared after the fire, but those

species had low cover and were ephemeral, and the community remained strongly dominated by

the pre-fire species assemblage (Keeley et al. 2005). Forests and woodlands in northern Australia

also exhibited little change in floristic composition after fire (Bowman et al. 1988), and a broad-

scale survey of Australian woody plants revealed that most species are capable of prompt post-

fire recovery via re-sprouting, fire-cued germination of a seed cohort, or both mechanisms

(Clarke et al. 2015). Nevertheless, other kinds of ecosystems do exhibit more complex

successional patterns and mechanisms. Pickett et al. (2001) concluded that neither the relay

floristics nor the initial floristic composition model adequately characterized the succession of

abandoned agricultural fields in the Buell-Small Succession Study in New Jersey; instead,

random "volleys" of species have arrived, persisting in some places and at some times but

quickly disappearing in others, reflecting stochastic differences in neighboring vegetation, edge

relationships, and fine-scale local environmental conditions.

Convergence and divergence. Evidence for divergence in YNP's plant community

composition over time was much stronger than evidence for convergence, again supporting the

importance of ecological memory for resilience of these forest communities to high-severity fire.

Recovering plant communities in areas of differing local climate and soils conditions differed in

species assemblages and plant morphological types during the initial post-fire years, and these differences persisted or became more pronounced over time. A previous study compared species composition after the 1988 fires in places where the time since the most recent fire prior to 1988 varied from 7-395 years; some minor differences in species richness and composition were related to fire intervals, but variation in local elevation and substrate was the dominant control (Schoennagel et al. 2003). Similarly, divergence in stand structure and species composition between steep and gentle topography was seen soon after fire in bishop pine (*Pinus muricata*) forests in California (Harvey and Holzman 2014), where serotinous cones in the pines and re-sprouting of dominant shrubs quickly re-established pre-fire stand structure and composition. However, a period of initial homogeneity followed by divergence in species composition of burned areas has been documented elsewhere, e.g., Douglas-fir forests of western Oregon (Halpern 1988), and may be more common in systems having a larger and more influential suite of early post-fire colonists than we saw in Yellowstone. Convergence over time in morphological types within a plant community may be more common in more mesic and fertile environments, such as the northern European study areas where such a trend has been observed (e.g., Kahmen and Poschlod 2004, Fukami et al. 2005), than in the relatively dry and infertile environment that characterizes Yellowstone.

Overall, we saw no evidence of either homogenization or introduction of novel species assemblages as a result of the Yellowstone fires: burn severity did not overwhelm the influence of biotic and informational legacies, and trends in species richness were not affected by patch size. Ecological memory may promote "precocious" development of early seral forests as plant

communities quickly recover compositional and structural complexity and diverge along environmental gradients (Donato et al. 2012).

Deterministic and stochastic influences. Deterministic variables that characterize the abiotic template—especially substrate, temperature and precipitation—were significant drivers of community composition in both 1999 and 2012, and their influences were similar in both years. Overall, species were more likely to occur (and thus species richness was likely to be greater) in locations with more fertile soils, warmer temperatures, and less annual precipitation. Interestingly, mean annual temperature increased in our study area between 1999 and 2012, which might have contributed to the continuing accumulation of new species at our higher elevation study areas after 2000. Some species may now be able to thrive at higher elevations than their pre-fire distributions, as observed for the cohort of seedling aspen that established throughout the burned landscape in 1989 (Hansen et al. 2016). The negative relationship between mean annual precipitation and occurrence of nearly all species was surprising initially, given that greater moisture availability usually promotes plant growth. However, most annual precipitation on the Yellowstone Plateau comes as snow, and the snowpack typically does not melt out until June. Greater precipitation therefore means more snow, longer-lasting snow cover, and a shorter growing season.

Of the two stochastic variables that influenced community composition after the 1988 fires, development of the post-fire lodgepole pine canopy was especially important. Lodgepole pine ANPP was significant in 1999 but less important than variables associated with the abiotic template. However, lodgepole pine density was the most important variable in 2012, with

negative effects on the occurrence of most understory species. The trees were small in 1999 (Turner et al. 2004) but much larger by 2012, when they formed nearly closed canopies in much of the burned area (Copenhaver and Tinker 2014, Turner et al. 2016a). As the trees continue to grow, their influence on the ground layer flora will likely increase. Following stand-replacing fire in a California forest, effects of the dominant post-fire canopy-forming species (bishop pine or *Ceanothus* spp. shrubs) also increased through time, as these species dictated the growing environment for other species (Harvey and Holzman 2014). However, in Douglas-fir–western hemlock forests in Oregon, effects of canopy closure on understory communities were surprisingly weak 40 years after logging and burning (Halpern and Lutz 2013). Longer-term study of the Yellowstone system is needed to evaluate the influence of continuing canopy development on ground-layer species composition.

The second stochastic influence on post-fire community composition in Yellowstone was burn severity, which was less important than the abiotic template and was short lived. The transient influence of burn severity in Yellowstone may reflect the nearly complete consumption of the surface litter layer, which resulted in similar post-fire soil conditions throughout areas of stand-replacing fire (Turner et al. 1997, 1999, 2003a, 2007) and only small initial differences in species composition among burn-severity classes. In contrast, variation in burn severity can be a much more important stochastic influence elsewhere, especially in systems that develop a deep organic horizon which strongly influences post-fire plant establishment. In boreal forests of North America and Scandinavia, the amount of residual organic matter (a measure of burn severity) is typically the major predictor of the long-term post-fire stand trajectory—either re-establishment of a conifer stand similar to the burned stand, where substantial organic matter

remains, or divergence toward deciduous forest or shrub-dominated vegetation where most organic matter is consumed by fire (Schimmel and Granstrom 1996, Johnstone et al. 2010 Siegwart Collier and Mallik 2010, Shenoy et al. 2011, 2013). These divergent trajectories are driven in part by different species traits, e.g., sprouting species are more prevalent where the burn is less severe, whereas obligate seeders do better on mineral soil, especially species having small seeds (Hollingsworth et al. 2013). The stand-level consequences of varying burn severity in these systems cascade up to the landscape level: the next fire in a deciduous forest developing after a locally severe burn typically exhibits more subdued fire behavior than does fire in a conifer forest, producing a negative feedback on fire behavior across the landscape (Johnstone et al. 2011).

A third stochastic predictor that was never significant in our study was distance from unburned forest, which reflects the size and shape of a burned patch. Although we initially hypothesized that unburned forests would be important propagule sources for post-fire recovery, off-site seed dispersal was a relatively unimportant recovery process—because most of the species in any given location survived the fire *in situ*. This result is consistent with the lack of effect of fire size on succession when biotic residuals are abundant as hypothesized by Turner et al. (1998) and further supports resilience of the native subalpine forest plant community to large, high-severity fire.

A potential stochastic influence and biotic legacy that we did not directly address in this study is composition of the soil seed bank, which has received little research attention but could be important in many settings (Brown et al. in press). The magnitude and species composition of

soil seed banks in temperate coniferous forests can vary immensely, both geographically and within a landscape (Abella and Springer 2012). Previous studies report huge differences, ranging from no seed bank in subarctic forest in the Northwest Territories, Canada (Johnson 1975), to few seeds in a subalpine forest in Colorado (Whipple 1978), to densities in the thousands of viable seeds per m^2 of soil surface in Douglas-fir and grand fir (*Abies grandis*) forests of central Idaho (Kramer and Johnson 1987). Soil seed banks were sampled in Yellowstone after the 1988 fires by Clark (1991), who found from tens to a few thousands of viable seeds m^{-2} in soils of unburned subalpine forests, representing a suite of species similar to what we documented in the post-fire forests. We observed few seedlings of herbaceous plants in the burned forests in 1989 and 1990, except for annuals, and excavations confirmed that, in those initial years, most of the perennial species in our sampling areas were re-sprouts (Turner et al. 1997). We began to see many more seedlings in 1991, but most of these likely came from seeds produced by the re-sprouting perennials that flowered prolifically beginning in 1990. The possible stochastic influence of local soil bank variation on post-fire vegetation patterns in Yellowstone remains unknown, but the paucity of seedlings (other than lodgepole pine seedlings) in post-fire years 1 and 2 in our study areas suggests a relatively small effect of seed bank variability.

Conclusions. Numerous studies have examined post-fire community development in subalpine forests, but most have dealt only with a limited portion of a burned landscape or followed the burned area only for a short time. Our dataset is unique in that it documents the first 25 years of post-fire development after a very large fire, based on permanent sampling points explicitly laid out to capture the range of spatial variability in underlying environmental characteristics and fire effects. Our sampling program was initiated soon after the fires and

sustained over 25 years—an optimal but rarely feasible opportunity in vegetation studies (Turner et al. 2003b, Driscoll et al. 2010, Lindenmayer et al. 2010). Further, because the study area is within a national park, we observed ecological dynamics with minimal anthropogenic interference, and our data can provide a valuable benchmark for comparison with other locations (Turner et al. 2016b). Future re-sampling of these plots may also allow effects of environmental change, such as climate warming, to be detected (e.g., Hansen et al. 2016).

The 1988 Yellowstone fires superimposed a spatially heterogeneous mosaic of burned patches and burn severities across a landscape underlain by broad variation in local climate and soils. Throughout the first 25 years, post-fire community development was strongly and consistently influenced by the abiotic template. Furthermore, post-fire patterns of community composition strongly resemble pre-fire patterns and have shown no signs of compositional convergence across the burned landscape. Variation in burn severity was of some importance for about a decade, but the burn mosaic clearly did not overpower the influence of the abiotic template and did not produce more spatially homogenous communities. Variation in the developing lodgepole pine canopy has now become a major driver of community composition, and whether the aggrading forest will act as a homogenizing force in the decades ahead is uncertain. Strong deterministic influences of the abiotic template probably are universal after fire, yet stochastic influences on succession vary among ecosystems and warrant additional research attention (White and Jentsch 2001). Although large, severe and notorious, the 1988 fires did not fundamentally alter subalpine forest plant communities in Yellowstone. Our data support the critical importance of ecological memory for ecosystem resilience to disturbance (Johnstone et al., in review). Whether these communities will be similarly resilient to future fires may

depend on whether fire regimes and climate remain within or depart from their historical ranges of variability.

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DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad:

http://dx.doi.org/10.5061/dryad.b1q0v

Table 1. Summary of the datasets employed in this study (see Figure 1 for locations).

Dataset	Years sampled	Sample types and sample sizes
Question 1 – Convergence and divergence		
Full patches dataset	1991, 1992, 1993, 1996, 2000	10-m^2 plots ($n = 552$) distributed among three burned patches (large, moderate, and small) located in each of three geographic areas (Table 2)
Severely burned patch centers	1991, 1992, 1993, 1996, 2000, 2013	10-m^2 plots ($n = 42$) in the severely burned center of the large or moderate patch in each of the three geographic areas
Question 2 - Processes		
Broadly distributed plots	1999, 2012	0.25-ha plots ($n = 72$) distributed randomly throughout the areas of stand-replacing fire

Table 2. Characteristics of the three geographic areas in Yellowstone National Park (YNP) where plant species presence was sampled in large, moderate, and small burned patches using 10-m^2 plots from 1991 to 2013. All were forested at the time of the 1988 fires (see Turner et al. 1997 and 2003a for additional details).

Characteristic	Cougar	Fern	Lake
General location	West-central YNP, forest near lower forest ecotone	Southwestern YNP, extensive forest near Old Faithful	Southeastern YNP, forest interspersed with meadows
Elevation (m)	2150-2300	2270-2500	2400-2700
Geologic substrate	Rhyolite and tuff (relatively infertile Quaternary volcanics)	Rhyolite (infertile Quaternary volcanics)	Quaternary lake sediments and andesite (somewhat fertile Eocene volcanics)
Pre-fire forest age	ca. 130-yr	ca. 250–290 yrs	ca 250–400 yrs
Characteristic species	Trees: *Pinus contorta*; shrubs: *Ceanothus velutinus*; herbs: *Calamagrostis rubescens*	Trees: *Pinus contorta*; shrubs: *Vaccinium scoparium*; herbs: *Carex geyeri, Lupinus argenteus*	Trees: *Pinus contorta, Abies lasiocarpa*; shrubs: *Vaccinium scoparium*; herbs: *Calamagrostis canadensis*
Patch size (number of 10-m^2 plots sampled)			
Large	500 ha (84 plots)	480 ha (103 plots)	3698 ha (59 plots)
Moderate patch	91 ha (46 plots)	200 ha (82 plots)	74 ha (67 plots)
Small patch	1 ha (34 plots)	1 ha (37 plots)	1 ha (40 plots)

Table 3. Statistics of community composition over time in three geographic areas that burned in the 1988 Yellowstone fires; see Figure 5. (a) Multiple response permutation procedures (MRPP) rank-transformed output of site-year within-group Sorensen distance (δ) among 10-m^2 plots over time for each of three geographic areas. Smaller values of δ signify tighter clustering, i.e., greater within-group similarity. (b) NMS Pearson and Kendall correlations of environmental variables with ordination axes in all 10-m^2 plots from 1991-2000 (n= 2830). (c) NMS Pearson and Kendall correlations of environmental variables with ordination axes in subset of 10-m^2 plots within centers of large or moderate-sized burn patches from 1991-2013 (n= 244) (See Table 1).

(a) Full patches data set

	Geographic area					
	Cougar		Lake		Fern	
Year	n	δ	n	δ	n	δ
1991	169	0.3680	225	0.3682	190	0.4108
1992	169	0.3246	225	0.3505	190	0.3801
1993	169	0.2581	225	0.3439	190	0.3309
1996	169	0.2923	224	0.3430	190	0.3252
2000	162	0.2727	222	0.2678	111	0.3351

(b) Full patches data set (1991 to 2000)

Variable	Axis 1			Axis 2			Axis 3		
	r	r^2	tau	r	r^2	tau	r	r^2	tau
Elevation	0.351	0.123	0.209	0.633	0.401	0.453	-0.069	0.005	-0.049
Burn severity	-0.106	0.011	-0.078	0.319	0.102	0.267	-0.326	0.106	-0.27
Lodgepole pine density	-0.212	0.045	-0.292	-0.255	0.065	-0.329	0.156	0.024	0.101

(c) Severely burned patch centers (1991 to 2013)

Variable	Axis 1			Axis 2			Axis 3		
	r	r^2	tau	r	r^2	tau	r	r^2	tau
Elevation	-0.809	0.654	-0.577	0.224	0.050	0.150	-0.126	0.016	-0.104
Lodgepole pine density	0.316	0.100	0.550	-0.299	0.089	-0.157	-0.031	0.001	0.09

Table 4. Species strongly and positively associated with a particular burn-severity class and negatively associated with a contrasting burn severity class, based on indicator species analysis. (Values of phi $\geq$ |0.20| indicate a strong association and are in bold.) None of the other species present in a given geographic area (Table 2) were strongly associated with a burn-severity class.

Species	Phi			Geographic area
	Low-severity surface fire	Severe surface fire	Crown fire	
Native tree, adults not fire-resistant, regenerates via post-fire seed dispersal				
Abies lasiocarpa	**0.454**	0.009	**-0.218**	Fern
	0.349	0.015	**-0.209**	Lake
Native tree, adults moderately fire-resistant, regenerates via post-fire seed dispersal				
Pseudotsuga menziesii	**0.430**	0.109	**-0.409**	Cougar
Native perennial forbs, regenerate via sprouting, small soil seed bank, and post-fire seed dispersal				
Antennaria racemosa	**0.289**	0.007	**-0.232**	Cougar
Aquilegia flavescens	**0.345**	0.153	**-0.289**	Lake
Chamerion angustifolium	0.077	**0.207**	**-0.226**	Cougar
Fragaria vesca	**0.207**	0.065	**-0.207**	Cougar
Fragaria virginiana	**0.375**	-0.124	**-0.210**	Cougar
	0.223	0.126	**-0.210**	Lake
Galium boreale	**0.253**	0.100	**-0.208**	Lake
Geranium viscosissimum	**0.275**	0.131	**-0.239**	Lake
Hieracium albiflorum	**0.298**	0.147	**-0.244**	Fern
Lupinus argenteus	**0.299**	0.115	**-0.254**	Lake
Osmorrhiza chilensis/depauperata	**0.443**	0.201	**-0.376**	Lake

Native perennial graminoids, regenerate via mix of sprouting + post-fire seed dispersal

Bromus ciliatus	**0.512**	0.106	**-0.359**	Lake
Carex geyeri	**0.315**	0.108	**-0.217**	Fern
	0.390	0.174	**-0.345**	Lake
Calamagrostis rubescens	0.165	**0.229**	**-0.334**	Cougar

Native perennial shrub, regenerates via sprouting + large heat-stimulated soil seed bank

Ceanothus velutinus	**-0.406**	-0.139	**0.450**	Cougar

Native perennial sedge, regenerates via sprouting + large heat-stimulated soil seed bank

Carex rossii	**-0.438**	-0.108	**0.432**	Cougar
	-0.319	-0.189	**0.326**	Lake

Native annual forbs, regenerate via mix of small soil seed bank + post-fire seed dispersal

Collinsia parviflora	**-0.313**	0.010	**0.247**	Cougar
Epilobium ciliatum	**-0.282**	-0.069	**0.211**	Lake
Gayophytum diffusum	**-0.386**	-0.164	**0.453**	Cougar
	-0.364	-0.138	**0.268**	Fern
	-0.308	-0.142	**0.303**	Lake
Polygonum douglasii	**-0.231**	-0.042	**0.229**	Cougar

Table 5. (a) Morphological types of species present in the centers of severely burned patches in three geographic areas (Table 2) in 1991 and in 2013. (b) Bray-Curtis dissimilarity indices (Bray and Curtis 1957), computed by treating morphological types as "species" and number of species within a morphological type as "density." The category "short-lived forbs" includes annuals, biennials, and short-lived perennials.

(a) Summary	1991		2013	
Morphological type	**No. species**	**% of species**	**No. species**	**% of species**
COUGAR lowest elevation, infertile substrates)				
Trees	2	7%	2	5%
Shrubs & subshrubs	4	15%	7	18%
Perennial forbs	14	54%	20	50%
Short-lived forbs	3	12%	5	12%
Perennial graminoids	3	12%	6	15%
Total	26	100%	40	100%
FERN (intermediate elevation, infertile substrates)				
Trees	3	13%	2	4%
Shrubs and subshrubs	1	4%	3	6%
Perennial forbs	12	52%	26	52%
Short-lived forbs	3	13%	4	8%
Perennial graminoids	4	18%	15	30%
Total	23	100%	50	100%
LAKE (highest elevation, fertile substrates)				
Trees	1	4%	5	7%

Shrubs and subshrubs	4	14%	7	9%
Perennial forbs	16	55%	39	53%
Short-lived forbs	3	10%	6	8%
Perennial graminoids	5	17%	17	23%
Total	29	100%	74	100%

(b) Bray-Curtis index of dissimilarity

	1991	2013
Cougar - Fern	0.57	0.61
Fern - Lake	0.60	0.60
Cougar – Lake	0.55	0.65
Mean dissimilarity	0.57	0.62

Table 6. Coefficients of fixed and random effects in the best (lowest AIC) multi-level model for plant species present in at least 5% of 72 broadly distributed burned plots (n = 58 species total) in *1999*, 11 years following the 1988 Yellowstone Fires. All plots were within stand-replacing fire. (a) Overall model indicates predictors related to presence of any species (fixed effects) and those that explain among-species variation in presence (random effects). (b) Coefficients of predictors for individual species are the random effect plus the estimate for fixed effects to account for the mean slope. Coefficients > |0.20| are interpreted as indicating strong effects and are in **bold** font. All predictors were standardized prior to analysis and therefore can be compared within the model. Some plants could be identified only to genus in the field, due to lack of flowers and fruits, but the most likely species epithet is indicated in parentheses based on observations of

distributions of the genus elsewhere throughout the burned forests. See Appendix S3 for species characteristics.

(a) Overall model for post-fire year 11 (*1999*)		
Variable	Fixed effects	Random effects
Intercept	-1.08***	0.19
Substrate	0.38***	0.30
Mean annual precipitation (1989-1998)	-0.27***	0.09
Lodgepole pine ANPP	-0.26***	--
Burn severity (dNBR)	0.16***	--
Mean annual temperature (1990-1999)	0.08***	0.11

*P < 0.05, **P < 0.01, ***P < 0.001

(b) Random effects coefficients by species after fixed effects have been added (*1999*).

Scientific Name	Substrate	Precipitation 1989-1998	Temperature 1990-1999
Achillea millefolium	-0.182	**-0.403**	**-0.249**
Achnatherum sp. (nelsonii?)	0.050	0.136	-0.041
Agoseris aurantiaca	**0.796**	**-0.415**	-0.069
Agoseris glauca	**0.287**	**-0.628**	**0.472**
Agropyron sp. (spicatum?)	**0.731**	-0.188	0.114
Agrostis scabra	0.151	-0.192	**-0.318**

Anaphalis margaritacea	**0.651**	**-0.285**	-0.087
Androsace septentrionalis	**0.355**	**0.339**	0.133
Antennaria microphylla	0.161	**-0.381**	-0.60
Antennaria racemosa	**0.734**	**-0.262**	**0.214**
Antennaria rosea	0.024	-0.179	-0.160
Arabis sp. (glabra or holboellii)	0.016	-0.002	-0.184
Arnica cordifolia	-0.001	**-0.303**	-0.040
Arnica latifolia	**0.869**	**-0.207**	0.100
Astragalus miser	**0.254**	-0.123	0.082
Bromus sp. (ciliatus?)	**1.197**	**-0.399**	0.064
Calamagrostis canadensis	**-0.240**	-0.150	**0.220**
Calamagrostis rubescens	**0.254**	**-0.478**	**-0.269**
Campanula rotundifolia	**0.885**	**-0.396**	**0.293**
Carex geyeri	**-0.277**	**-0.345**	0.000
Carex ovales group (Carex spp)	**1.202**	**-0.395**	0.181
Carex rossii	-0.032	**-0.290**	**-0.748**
Chamerion angustifolium	-0.031	**-0.615**	0.055
Cirsium arvense	**0.475**	-0.148	**-0.217**
Collinsia parviflora	**0.775**	**-0.287**	**0.216**
Collomia linearis	**0.662**	**-0.492**	**0.480**
Crepis sp. (tectorum?)	**0.639**	-0.165	**0.230**
Elymus elymoides	**0.673**	**-0.216**	0.116
Epilobium ciliatum	**0.533**	-0.437	-0.124

Eurybia merita	**0.322**	**-0.612**	0.111
Eurybia integrifolia	**1.216**	-0.136	0.078
Eurybia sp. (not E. merita or integrifolia)	0.182	-0.162	-0.070
Fragaria vesca	**0.517**	0.110	0.019
Fragaria virginiana	**0.479**	0.017	-0.026
Galium boreale	**0.617**	**-0.311**	**0.761**
Gayophytum diffusum	0.003	**-0.726**	0.093
Gentianella amarella	**0.209**	**-0.327**	-0.008
Geranium sp. (richardsonii or viscosissimum)	**0.927**	-0.180	0.081
Hieracium albiflorum	-0.004	-0.164	**-0.331**
Hieracium triste var. gracile	0.099	**-0.428**	**0.479**
Juncus sp.	**1.088**	**-0.264**	0.030
Linnea borealis	**0.585**	-0.169	0.158
Lupinus argenteus	0.184	**-0.590**	0.106
Machaeranthera canescens	**0.953**	**-0.299**	**0.226**
Penstemon sp. (procera?)	**0.471**	**-0.301**	**0.327**
Phleum pratense	**0.221**	**-0.345**	**0.345**
Phlox sp. (hoodii or longifolia?)	**0.782**	**-0.322**	**0.382**
Poa sp. (nervosa?)	0.145	**-0.493**	**0.508**
Polygonum douglasii	**0.856**	**-0.318**	0.076
Potentilla sp. (diversifolia or gracilis)	**0.682**	**-0.272**	0.143
Pseudognaphalium macounii	0.102	-0.160	**0.344**
Solidago sp. (missouriensis or multiradiata)	0.021	**-0.216**	**0.204**

Spiraea betulifolia	**0.798**	-0.199	0.120
Taraxacum officinale	-0.176	**-0.243**	-0.091
Thalictrum sp. (fendleri or occidentale?)	**0.955**	-0.177	**0.374**
Trisetum spicatum	**-0.545**	0.052	-0.119
Vaccinium scoparium	0.102	0.038	0.081
Viola sp. (adunca?)	**0.501**	**-0.357**	**0.202**

Table 7: Coefficients of fixed and random effects in the best (lowest AIC) multi-level model for plant species present in at least 5% of 72 broadly distributed burned plots (n = 52 species total) in *2012*, 24 years following the 1988 Yellowstone Fires. See caption for Table 6 for explanation.

(a) Overall model for post-fire year 24 (*2012*)		
Variable	Fixed effects	Random effects
Intercept	-1.19***	0.19
log (Pine density)	-0.55***	0.36
Substrate	0.40***	0.24
Mean annual precipitation (2002-2011)	-0.22**	0.10
Elevation	--	0.23
Mean annual temperature (2003-2012)	0.18*	0.14

*P < 0.05, **P < 0.01, ***P < 0.001

(b) Random effects coefficients by species (*2012*)

Scientific Name	Log pine ANPP	Substrate	Precipitation 2002-2011	Elevation	Temperature 2003-2012
Achillea millefolium	**-1.107**	**0.217**	**-0.272**	-0.155	0.029
Achnatherum sp. (nelsonii?)	**-1.196**	-0.066	**0.209**	0.189	0.089
Agoseris glauca	**-0.732**	0.193	**-0.262**	0.017	-0.010
Agrostis scabra	**-0.953**	**0.229**	-0.014	**0.431**	**0.314**
Anaphalis margaritacea	**-0.710**	**1.035**	**-0.209**	-0.083	0.126
Antennaria microphylla	**-0.805**	-0.029	**-0.501**	**-0.359**	**-0.308**
Antennaria racemosa	-0.048	**0.319**	**-0.303**	**0.285**	**0.535**
Antennaria rosea	**-0.570**	**0.665**	-0.095	**-0.276**	**0.223**
Arabis sp. (glabra or holboellii)	**-0.847**	**0.495**	**-0.546**	**-0.509**	0.013
Arnica cordifolia	0.141	0.016	**-0.418**	**0.259**	-0.001
Astragalus miser	-0.026	**0.806**	**-0.506**	-0.011	**0.445**
Calamagrostis canadensis	**0.241**	**0.359**	-0.142	**0.209**	**-0.235**

Calamagrostis rubescens	**0.421**	0.028	**-0.523**	**-0.309**	**0.225**
Campanula rotundifolia	**-0.418**	**0.277**	**-0.404**	**-0.737**	**0.312**
Carex geyeri	**-0.342**	**-0.268**	-0.035	**-0.294**	**-0.257**
Carex ovales group (Carex spp)	**-0.928**	**0.405**	-0.034	-0.188	**0.426**
Carex rossii	**-1.006**	-0.117	**-0.444**	**0.333**	0.016
Chamerion angustifolium	**-0.655**	-0.039	**-0.764**	0.019	**-0.446**
Collinsia parviflora	**-0.835**	0.138	**-0.483**	**-0.569**	**0.387**
Collomia linearis	**-0.746**	**0.563**	**-0.364**	**-0.387**	**0.399**
Crepis sp. (tectorum?)	**-1.027**	**0.568**	**0.205**	0.109	**0.467**
Elymus elymoides	**-1.201**	**0.692**	**-0.423**	**-0.457**	0.199
Epilobium ciliatum	**-0.545**	**0.770**	-0.180	-0.107	0.175
Eriogonum umbellatum	**-0.985**	**0.228**	**0.210**	**0.515**	**0.495**
Eurybia merita	**-0.984**	0.180	**-0.579**	**-0.497**	**0.240**
Eurybia sp. (not merita or integrifolia)	**-0.391**	**1.080**	**-0.267**	0.047	**0.425**
Fragaria virginiana	**-0.314**	**0.412**	**-0.523**	**-0.270**	**-0.212**
Galium boreale	**-0.639**	**1.291**	**-0.204**	**-0.302**	**0.251**

Gayophytum diffusum	**-1.737**	**0.211**	**-0.244**	**-0.617**	-0.082
Gentianella amarella	-0.188	**0.732**	-0.095	-0.182	0.165
Geranium sp. (richardsonii or *viscosissimum)*	-0.125	**0.633**	-0.124	-0.051	**0.278**
Hieracium albiflorum	**-1.000**	**-0.297**	-0.087	**0.717**	0.169
Juncus sp.	**-0.722**	**0.307**	**0.232**	**0.371**	**0.481**
Linnea borealis	-0.075	**0.371**	-0.075	-0.147	**0.225**
Lupinus argenteus	**-0.600**	0.149	**-0.482**	**-0.355**	**-0.231**
Mahonia repens	-0.146	0.136	-0.198	**-0.602**	0.596
Penstemon sp. (procera?)	0.119	**0.818**	-0.190	-0.129	**0.251**
Phleum alpinum	**-0.374**	**1.101**	-0.180	0.293	**0.476**
Phlox sp. (P. hoodii or longifolia?)	**-0.548**	**0.535**	-0.096	-0.128	**0.276**
Poa sp. (nervosa?)	**-0.454**	**0.403**	-0.049	**0.384**	0.157
Polygonum douglasii	**-1.040**	**0.829**	**-0.227**	0.114	**0.395**
Potentilla sp. (diversifolia or gracilis)	**-0.388**	**0.593**	**-0.252**	-0.073	**0.254**
Rumex acetosella	**-0.481**	**0.314**	-0.088	-0.026	**0.439**
Salix sp. (scouleriana?)	-0.165	**0.633**	-0.129	-0.173	**0.254**

Senecio sp. (serra or triangularis?)	**-1.067**	**0.521**	0.198	0.052	**0.542**
Solidago sp. (missouriensis or multiradiata)	**-0.222**	0.022	-0.187	-0.119	**-0.344**
Spiraea betulifolia	0.002	0.137	**-0.244**	0.033	**0.484**
Taraxacum officinale	**-0.490**	0.188	**-0.431**	-0.024	**-0.212**
Thalictrum sp. (fendleri or occidentale?)	**-0.375**	**1.168**	-0.189	0.100	**0.383**
Trisetum spicatum	**-1.238**	0.038	0.166	**0.277**	0.094
Vaccinium scoparium	0.079	-0.007	-0.198	**0.824**	-0.142
Viola sp. (adunca?)	0.049	**0.702**	**-0.299**	-0.021	0.037

Table 8. Plant species that increased or decreased substantially in abundance (i.e., that increased or decreased by ≥50% in proportion of plots in which it was recorded) from 1999 to 2012 in 72 0.25-ha plots broadly distributed across the areas that burned as stand-replacing fire in the 1988 Yellowstone fires.

Species characteristics	Plots where present (%)		Species
	1999	2012	
Species that decreased substantially from post-fire years 11 to 24			
Annuals, biennials, or short-lived perennials	4	0	*Androsace septentionalis*
	29	14	*Collomia lineata*
	17	7	*Gentiana amarella*
	31	14	*Epilobium ciliatum*
Long-lived perennial grasses typical of grasslands and other non-forest environments	13	1	*Agropyron* sp.
	4	0	*Phleum pratense*
Long-lived perennial forbs, relatively shade intolerant, typical of various environments	25	8	*Antennaria rosea*
	25	4	*Cirsium arvense*
Long-lived perennial grasses of unknown shade tolerance, typical of forest environments	72	29	*Agrostis scabra*
	14	1	*Bromus* sp.
	54	25	*Poa* sp.
	82	4	*Trisetum spicatum*
Long-lived perennial forbs of moderate shade	24	3	*Fragaria vesca*

tolerance, typical of forest environments

Long-lived perennial forbs of unknown shade	15	3	*Arnica latifolia*
tolerance, typical of forest environments	14	1	*Spirea betulifolia*
	25	1	*Agoseris aurantiaca*
	6	0	*Claytonia lanceolate*
	8	8	*Eurybia integrifolia*
	15	4	*Hieracium triste* var. *gracile*
	8	0	*Machaeranthera canescens*
	19	1	*Pseudognaphalium macounii*

Species that increased from post-fire years 11 to 24

Long-lived perennial forb of moderate shade	4	7	*Thalictrum* sp.
tolerance, typical of forest environments			
Long-lived perennial forb of unknown shade	10	21	*Astragalus miser*
tolerance, typical of forest environments	4	11	*Eriogonum umbellatum*

Table 9. Characteristic species of mature forests in the three geographic areas of our post-1988 study, based on (i) published distribution maps of forest habitat types and (ii) our unpublished records from unburned forests in YNP. We also indicate whether the species was observed following the 1988 fires in our data from this study. Sources (D, G, L, N, S, W) are identified below, and *Post-88* refers to this study.

	Cougar	Fern	Lake
Abies lasiocarpa	S, *Post-88*	D, L, S, *Post-88*	D, S, W, *Post-88*
Achillea millefolium	D, *Post-88*	--	--
Agoseris glauca	G, *Post-88*	--	--
Antennaria microphylla	N, *Post-88*	--	--
Antennaria racemosa	--	--	D, *Post-88*
Arnica cordifolia	D, G, *Post-88*	D, S, *Post-88*	D, S, W, *Post-88*
Calamagrostis canadensis	--	S, *Post-88*	S, *Post-88*
Calamagrostis rubescens	D, G, S, *Post-88*	--	--
Campanula rotundifolia	G, *Post-88*	--	--
Carex geyeri	G, N, S, *Post-88*	D, N, L, *Post-88*	W, *Post-88*
Chamerion (Epilobium) angustifolium	G, *Post-88*	D, L, *Post-88*	D, W *Post-88*
Chimaphila umbellatum	--	--	W
Danthonia intermedia	--	--	W, *Post-88*
Equisetum arvense	--	--	D, *Post-88*
Eurybia (Aster) integrifolius	--	--	W, *Post-88*
Fragaria vesca	D, G, *Post-88*	--	W, *Post-88*
Fragaria virginiana	--	--	W, *Post-88*
Geranium viscosissimum	D, S, *Post-88*	--	--

Hieracium albiflorum	N, *Post-88*	--	W, *Post-88*
Linnea borealis	--	--	D, S, *Post-88*
Lonicera utahensis	--	--	D, S, W, *Post-88*
Lupinus argenteus	G, *Post-88*	L, *Post-88*	W, *Post-88*
Luzula parviflora	--	--	D, *Post-88*
Mahonia repens	--	--	W, *Post-88*
Osmorhiza chilensis	--	D	W, *Post-88*
Pachystima myrsinites	S[1]	--	--
Parnassia fimbrinata	--	--	D, *Post-88*
Pedicularis racemosa	--	S	S, *Post-88*
Picea engelmannii	--	D, L, S, *Post-88*	D, S, W, *Post-88*
Pinus albicaulis	--	L	--
Pinus contorta	D, G, S, *Post-88*	L, S, *Post-88*	D, S, W, *Post-88*
Populus tremuloides	D, *Post-88*	--	--
Pseudotsuga menziesii	D, S, *Post-88*	D[2]	D[2]
Pyrola (Orthilia) secunda	--	D, S	D, S, W, *Post-88*
Ribes montigenum	--	D	--
Senecio triangularis	--	--	D, *Post-88*
Solidago multiradiata	--	N, *Post-88*	--
Spirea betulifolia	D, S, *Post-88*	--	--
Streptopus amplexifolius	--	--	D, *Post-88*
Symphoricarpos oreophilum	S, *Post-88*	--	--
Thalictrum occidentale	--	D, *Post-88*[3]	--
Vaccinium scoparium	S, *Post-88*	D, L, S, *Post-88*	D, S, W, *Post-88*
Viola adunca	S, *Post-88*[4]	--	--

D = indicator species of Despain's (1990) habitat types in YNP that spatially overlap our study areas in YNP … **Cougar**: Douglas-fir/pinegrass habitat type … **Fern**: subalpine fir/grouse whortleberry, subalpine fir/elksedge, and subalpine fir/bluejoint reedgrass habitat types … **Lake**: subalpine fir/twinflower, and Engelmann spruce/common horsetail habitat types.

G = species recorded as "common" in both of two 0.25-ha plots of mature forest in the Rockefeller Parkway just south of YNP, with elevation and substrate similar to the **Cougar** study area (Romme et al., unpublished data, 2004).

L = species recorded as present in >50% of 33 stands sampled for fire history in the Little Firehole watershed, with elevation and substrate similar to the **Fern** study area (Romme, unpublished data, 1977).

N = species present in $\geq$50% of eight mature stands sampled near our **Fern** study area, or species present in both of two stands near our **Cougar** study area, in a survey of inorganic nitrogen availability and N stocks (unpublished data, Turner et al.).

S = indicator species of Steele et al.'s (1983) habitat types in eastern Idaho and western Wyoming that spatially overlap our study areas in YNP… **Cougar**: PSME/SPBE CARU phase, PSME/CARU CARU phase, and ABLA/VASC CARU phase … **Fern**: ABLA/CACA and ABLA/VASC … **Lake**: ABLA/CACA, ABLA/LIBO VASC phase, and ABLA/VASC VASC phase

W = species recorded as "common" in all of three 0.25-ha plots of mature forest near the West Thumb of Yellowstone Lake, with elevation and substrate similar to the **Lake** study area (Romme et al., unpublished data, 2004).

Post-88 = species recorded in each of the three geographic areas (**Cougar**, **Fern**, and **Lake**) during the course of the present study.

[1] Steele et al.'s habitat types apply to a large area in eastern Idaho and western Wyoming, and although indicator species are characteristic of much of that area, they are not necessarily present throughout. Notably, *Pachystima* (*Paxistima*) *myrsinites* is rare or absent in northwestern Wyoming (Dorn 2001) and was probably not present in our Cougar study area even before the 1988 fires.

[2] Despain's habitat types apply to all of YNP. *Pseudotsuga menziesii* is common within his subalpine fir/twinflower habitat type in some parts of YNP, especially on high-elevation andesite substrates (personal observations), but is not present in all areas mapped as this habitat type, including our Fern and Lake study areas. During field work from 1977-1987 (prior to the 1988 fires), Romme noted the absence of *Pseudotsuga* in these two areas. Thus, the post-fire lack of *Pseudotsuga* at Fern and Lake does not represent a failure of regeneration in these areas.

[3] *Thalictrum* sp. in our data-set.

[4] *Viola* sp. in our data-set.

FIGURE LEGENDS

Figure 1. Map of Yellowstone National Park, Wyoming (USA) showing locations of burned patches sampled in 1991-2013 (small, moderate, and large circles in each of three geographic areas) and broadly distributed burned plots sampled in 1999 and 2012 (triangles). Shaded area represents the general outlines of the 1988 fires.

Figure 2. Species richness from 1991-2000 by geographic area (see Figure 1, Table 2), based on rarefaction curves (see Appendix S2) using the sample size of the area having the smallest number of samples for all of the areas being compared.

Figure 3.   Species richness from 1991-2000 by patch size within each geographic area (see Figure 1, Table 2), based on rarefaction curves (see Appendix S2) using the sample size of the patch having the smallest number of samples for all of the patches being compared. (a) Cougar area, infertile, lowest elevation. (b) Fern area, infertile, intermediate elevation. (c) Lake area, more fertile, highest elevation.

Figure 4.   Species richness from 1991-2013 in the centers of severely burned patches in three geographic areas; n=14 plots in each area in each year (see Table 1). The Cougar area is infertile and at lowest elevation; the Fern area is infertile and at intermediate elevation, and the Lake area is more fertile and at highest elevation (see Figure 1, Table 2). (a) Mean number of vascular plant species per 10-m^2 plot. (b) Number of vascular plant species recorded among all 10-m^2 plots within a given geographic location; (c) Total number of species among all sample plots from all three geographic areas from 1991-2013..

Figure 5.   Non-metric Multidimensional Scaling ordination plot of axes 1 and 2 for permanent 10-m^2 plots that were sampled periodically from 1991-2013 for species presence in three geographic areas (Figure 1, Table 2) after the 1988 Yellowstone fires. Open circles are species and crosses are site-year group mean values with error bars that represent the inter-quartile range surrounding the mean. (a) All plots sampled from 1991-2000. (b) Subset of plots sampled in the centers of severely burned patches from 1991-2013 (see Table 1).